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# Responses of Young-Mature Conifers to 12 and 13 Years of Moisture Stress

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# RESPONSES OF YOUNG-MATURE CONIFERS TO 12 AND 13 YEARS OF MOISTURE STRESS

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Supplement #13
University of Idaho

Abstract: McMINN, Robert G., LEAPHART, Charles D., and LOEWENSTEIN, Howard. 1975. Responses of young-mature conifers to 12 and 13 years of moisture stress. Can. J. For. Res. ________.

Young-mature conifers were subjected to increased moisture stress by sheltering their root systems from precipitation, either continuously or seasonally, for 12 and 13 years. These treatments were to determine whether the symptoms of pole blight, a disease of pole-sized western white pine, could be induced experimentally. Reduction in height and radial increments and foliage weight occurred in treated trees compared with untreated trees. However, no stem lesions, the most diagnostic symptom of pole blight, were found. Although reduction in root length was likewise not detected, greater mortality among 2-5 mm roots was apparent. Soil moisture in the upper horizons of the continuously sheltered plots was reduced to low levels by the end of the first growing season. Moisture at depths greater than 120 cm was relatively unaffected by sheltering. This supply of moisture at greater depths probably was a significant factor mitigating moisture stress and preventing development of the full range of pole blight symptoms.

## INTRODUCTION

Wherever trees of indigenous species grow, their growth, health and vigor are chiefly conditioned by the availability of moisture (2). No other element has been so limiting to the well being of these trees over a continuum of days, years, or centuries. Yet, they manage somehow to survive a variety of moisture-stress circumstances.

If the pole blight of western white pine (*Pinus monticola* Dougl.), a disease of unknown cause, is induced by moisture stress factors (6,8,11), we reasoned that we might cause the disease by artificially imposing drought-like conditions on trees of susceptible age. Copeland (2) found that a 5-year artificially-induced drought resulted in crown symptoms on shortleaf pine (*P. echinata* Mill.) characteristic of the little-leaf disease, except chlorosis was lacking. The imposed drought reduced needle length and retention, caused a cessation of radial growth, and lowered available moisture of the soil considerably below the original level. Our study evaluates the responses of white pine and other species to a similarly imposed drought for periods of 12 and 13 years.

## METHODS

### Plot Installation and Dismantling

A gently sloping, accessible site, well stocked with healthy, pole-size trees, particularly white pine, was chosen on the Priest River Experimental Forest in northern Idaho. The site is located in a *Tsuga heterophylla*/*Pachistima myrsinites* habitat in which the predominant climax tree species occurs as an understory. The soil profile throughout the study area is characterized by loose loams in the upper 30 to 40 cm with an abrupt transition to a lacustrine deposit of a silty clay loam layer of about 60 cm underlain with interspersed layers of dense loams, sands, or clays of varying thicknesses.

Four treatments were compared; two, permanent A and control, were installed in 1955 and two, permanent B and seasonal, in 1956. All were within 150 m of each other and about 9x16 m in size. The objective of both permanent A and B treatments was to exclude fall-through precipitation and surface water from the trees on the treated units. This was accomplished by building a wooden shelter around the trees (Fig. 1) for permanent A and by laying a polyethylene cover of about 0.15 mm thickness on the smoothed ground around the trees for permanent B. The plastic was replaced whenever it had deteriorated enough so water could enter the soil beneath it. The seasonal treatment's objective was to exclude the same type of water from the plot from June 22 to September 22 (an average with a range of 4/8 to 7/10 and 9/10 to 10/10) and was achieved by laying plastic similar to permanent B around the trees for that approximate time period each year of the study. Fences were built around both plastic-covered plots to prevent animal damage to the plastic. Trenches were dug to a depth of 1 m around all sheltered plots in a manner to rapidly conduct water away from them. The control (Fig. 2) had no covering nor was it trenched.

All trees except white pine were cut at ground line and removed from the control and permanent A plots prior to shelter construction. Eleven trees were left on the control and 10 on the other plot. Only dead trees were removed at ground line before the plastic was placed on the seasonal and permanent B plots. Four white pine, two Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco], two western larch (Larix occidentalis Nutt.), and four western redcedar (Thuja plicata Donn.) trees remained in 1956 on the seasonal plot. On the permanent B plot, there were three white pine, four Douglas-fir, three larch, eight redcedar, one lodgepole pine (P. contorta Dougl.), and one western hemlock [Tsuga heterophylla (Rafn.) Sarg.]. Trees of the latter two species, which were not represented in any other plot, were not measured or used in subsequent analyses.

The trenches, shelters, and fences were maintained or replaced periodically as needed. Trees were removed as they died, i.e., none on the wooden shelter and control plots, a 10-cm d.b.h. Douglas-fir and an 18-cm larch on the permanent plot, and an 11-cm white pine and a 36-cm larch (killed by lightning) on the temporary plot; all died in 1961 or 1962.

All shelters were removed starting in early June 1968. By mid-July, all trees had been felled and measured, and their above-ground portions (excluding 0.5-m stumps) were removed from all four plots. Drainage pits had been dug to provide settling basins so that soil washed from the root systems did not enter the nearby creek. Hydraulic excavation and all root measurements were completed by mid-September.

## Sampling Procedures

Soil Moisture. Except for 1958 and 1959, each spring and fall until study termination, soil samples were taken from all plots at a minimum of two points per plot using King tubes. Cores were taken to 183 cm by 15.24-cm units, except when excess moisture prevented core extraction. Moisture contents were determined by oven-drying to 105°C and weighing. Laboratory measurements of the available water-holding capacity were made by the pressure plate method for each soil depth sampled, thus, providing a basis for plotting moisture depletion and replenishment rate data. These data were computed as cm of water per 15.24 cm of soil. All holes made by the sampling tubes were backfilled; and wire pins inserted in the backfilled holes as a precaution against resampling at those points.

Heights and Diameters. Larger white pine were lowered by a special procedure (5) to prevent breakage. All other species were felled directly and limbed. On the latter, only total height was measured and 1-inch discs were collected by cross-sectioning the stem every 1.5 m, starting at the butt cut. The remainder of the above-ground portion was discarded. In addition to measuring total height on white pine, annual growth segments between each node beginning with the 1967 one were measured as far down the stem as segments could be determined accurately.

One-inch discs were removed from white pine in the same manner as with the other species. For all species, the discs at every 3 m, starting at 0.5 m, were later sanded. Annual rings from 1944 through 1967 were measured along two average radii, each in at least a different quarter to provide diameter increments.

Stem Abnormalities. After the 1.5-m bolts were cut on the white pine, the bark was peeled from each. Any abnormality on the wood surface, with particular attention given to possible pole blight lesions, was diagrammed.

<u>Needle Length.</u> Needle lengths were based on all needles of a 10-fascicle sample. Each fascicle was chosen at random for each of the 3 to 5 years present from the main stem, from branches at each of the five uppermost nodes (1963 through 1967), and from branches at the 10th, 15th, and 20th nodes (1958, 1953, and 1948, respectively). The measurement used in later analyses was an average length of the needles in the 10 fascicles.

<u>Foliage Weight.</u> Foliage weights were determined from a subsample of tassels taken throughout the crown. Tassels in pine are the needle bearing portion of the stem and branches and are discrete from one another since the needles occur as clusters, or tassels. All tassels were clipped from all branches (and stem) of the five uppermost nodes (1963-1967) and from all branches at every fifth node down the stem starting at the 10th (1958) node. The adjacent node above or below was used if the fifth was atypical. Because order of parent branch affected tassel weight, tassels from each node were segregated into two groups, (1) from branches of primary or secondary origin and (2) from tertiary and higher order branches. If more than 20 tassels were present for all branches at each node, a 20-tassel sample was drawn randomly from the two tassel group proportionate to each number in them. Foliage was then stripped from this sample by years and oven dried to obtain the weight for the samples. Total foliage weight by years for each selected node was obtained by the formula: (total number tassels ÷ 20) x weight of 20-tassel samples. Since each node represented from 4 to 6 nodes, total foliage weight for the tree was computed by totaling the products (weight of each sample node x number of nodes represented).

Roots. After all tops had been measured and removed, stumps were secured to support them in place while the soil was washed from their roots (Fig. 3). Roots were excavated and supported by methods described by McMinn (10).

Measurements of roots on species other than white pine were estimated only (6). For white pine roots, laterals were measured in 1.0-2.0, 2.1-5.0, 5.1-10.0, and >10 cm diameter classes. Verticals were not differentiated by size classes; only their total length to 1 cm was recorded. However, we classified these lengths as either central roots (originating directly from the root collar) or branch roots of the central roots. Three vertical and three lateral roots chosen at random were measured in their entirety from the root collar to their 0.2-cm terminals, thus obtaining data for the 0.2 to <0.5 and 0.5 to <1.0 cm diameter classes. The data on these two classes were recorded by diameter of their parent roots, i.e., by one of the four larger classes plus the 0.5 to <1.0 class for the laterals, and by 0.5 to <1.0 and ≥1.0 classes for verticals. These base data for the six roots were used for converting measurements taken to 1 cm on all roots to a total root length by diameter class for laterals and verticals for each tree.

Root mortality was determined by diameter class for lateral and vertical roots. Each whole root segment within each class was tallied as one root and whether it was live or dead at the small end. Mortality was expressed as a percentage of the total roots being dead within each class by tree.

## RESULTS

### Crown and Stem Characteristics

Pole blight symptoms are specifically described elsewhere (1); but, briefly, they are as follows: Upper crown needles become chlorotic and are reduced in length. Terminal growth of stem and upper crown branches is reduced, often coinciding with reduced and irregular radial growth in the stem. As the branch terminal growth tends to slow down, the branch foliage tends to tuft at the terminals in lion's tail effects. As these foliar and branch growth symptoms progress down the crown over time, the top progressively dies back. An invariable symptom, which may precede, coincide with, or follow crown and growth symptoms, is development of lesions, or necrotic strips of cambium, which can vary from a few centimeters to more than 20 m in length. Resinosis accompanies the lesions on the stems.

No treatment induced all the crown and stem symptoms of pole blight in white pine. We found no lesions or resinosis and no abnormal (compared to control trees) discoloration of foliage attributable to the imposed moisture stresses. Terminal growth reduction was more noticeable and tufting of foliage on branch terminals tended to be more frequent on the treated (Fig. 4) than control trees. However, needle length, though generally shorter on stressed trees, was not significantly different among years or treatments, i.e., it averaged 7.9, 8.1, and 8.0 mm long on 1967, 1966, and 1965 foliage, respectively, of the control trees; and, correspondingly, 7.9, 7.3, and 7.4 on the permanent A; 7.7, 7.5, and 8.0 on the permanent B; and 8.3, 7.8, and 7.3 of the seasonal trees.

Crowns of species other than white pine on the seasonal and permanent plots appeared as normal as their counterparts off the plots, except for terminal growth rates. None had developed chlorosis or appeared to have lost abnormal amounts of foliage. Death of the few trees, previously mentioned, could not be attributed to stress treatments.

## Diameter and Height Growth Responses

Among the variables measured on white pine, the effect of treatment was most pronounced on radial and terminal growth (Table 1). The annual radial growth increased from the bottoms to the tops of the tree crowns in all treatments for both the prestress (1944-55) and stress (1956-67) periods, as has been found elsewhere (13), but was markedly lower for the stress periods in all treatments, particularly in the trees in permanent A and B. Analysis of variance on the annual basal area increment (ABAI) of the stress period divided by the ABAI of the prestress period, at 3.5 m (Table 2), confirmed these differences among treatments to be significant.

The transition from the prestress to the stress period in 1956 for permanent A trees and in 1957 for permanent B trees is abrupt (Fig. 5). In contrast to the control trees, the deviations of annual growth from the treatment means for permanent A and B trees are consistently negative for the stress period and positive for the pre-stress period (1944 to 1955 or 1956). Although the trees on the seasonal plot tend to follow the same pattern as for those in these two treatments, the pattern of deviation is more variable, as the analysis of variance verified.

Annual height growth responded to treatment similarly to radial growth, i.e., during the stress period, trees on permanent A and B plots averaged less than half the growth of the prestress period (Table 1). Growth on the seasonal plot ranged between that on these plots and the control.

Only total height was measured on species other than white pine. However, annual radial growth measurements were made on all of them in the same manner as for white pine. One Douglas-fir, one western larch, and four western redcedar dominant or codominant trees off the plots were selected as control trees. The growth of these trees was compared with 2 larches, 1 Douglas-fir, and 4 cedars on the seasonal plot and with 3 larches, 3 firs, and 8 cedars on the permanent B one. As with white pine, radial growth of these trees in the stress period (1957 through 1967) was reduced according to the type of treatment imposed. In particular, those trees on the permanent plot showed a dramatic reduction, as Table 3 shows.

## Root Mortality

Mortality within the root systems was highly variable among treatments (Table 4). Consequently, significant differences in mortality within any root diameter class among treatments was only observed in the 0.2 - <0.5 class of the lateral roots. This difference between the permanent B and seasonal plots was not interpretable.

## Root Depths

The percentages of vertical roots on the 12 dominant and codominant trees (Table 4) reaching into the successive 50-cm soil depths are tabulated by treatments and root diameters in Table 5. A few verticals of all of these trees penetrated the 200- to 250-cm depth. Only on the seasonal plot did a significant number (25%) penetrate beyond 250 cm. With the exception of one tree, major verticals were sound and healthy on all of these trees. That exception, a 30.6-cm diameter tree (stump height) located on the seasonal plot, had 9 of its major verticals completely rotted to the root collar by *Armillaria mellea* (Vahl. ex Fr.) Karst.

Detailed root measurements were not made on all intermediate and suppressed white pines nor on any trees of the other species. However, no verticals of any subdominant white pine penetrated to the 200 cm depth. Regardless of tree dominance, no vertical roots of trees of other species penetrated to the 200-cm depth; most had terminated before or at 150 cm.

Verticals of white pine were clubby or flattened, indicating a compact subsurface horizon difficult for penetration by roots (Fig. 6). Soil bulk density for the four plots averaged 1.62 in the 30.5- to 61.0-cm layer (a silty clay loam) and decreased to 1.48 at the 152.4- to 182.9-cm layer. Verticals tended to follow natural cleavage planes down through the dense soil layers and branched out, proliferated, and assumed more normal configuration in sand layers. Although narrow, sand or sandy loams, silt loam, and silt layers were common (Fig. 7), particularly below the 150-cm depth, roots usually proliferated in the broader ones, such as a 20-cm layer at 170-190 cm in the control plot, a 15-cm layer at 250 cm in the temporary cover plot, or a 10-cm layer at 105 cm in the permanent cover plot (Fig. 8).

Root Lengths

The mean length of lateral roots of dominant and codominant white pines were significantly different only in the 0.5-<1.0 diameter classes (Table 4). Significant differences existed among treatment means only in the 0.5-<1.0 diameter class of the lateral system. The great variation among trees within and among treatments accounts for the lack of significant differences attributable to treatment and is illustrated by the two large trees in the seasonal plot (Fig. 9). These two trees, one 38 m tall and 43 cm in diameter at the stump and the other 31 m and 31 cm, differed greatly in root lengths. The larger tree had 3.1 times as long a vertical and 2.5 times as long a lateral system as the smaller one. Interestingly, foliage weight was only 1.8 times greater for the larger than the smaller tree.

## Root Grafting

No interspecific root grafts were found. Also, no intraspecific grafts were found between trees on the seasonal and permanent B plots, but they were noted within trees of white pine and Douglas-fir. Grafting between (Fig. 10) and within (Figs. 10 and 11) the white pine on the control and permanent A plots was infrequent but important. For example, two trees in the latter were grafted in the root collar zone so extensively that their root systems were considered as one for analyses in this study. Two suppressed trees had died above ground in permanet A prior to plot establishment. However, their root systems were living because some laterals were grafted to other trees within the plot, i.e., these root systems were presumably being utilized by trees living when the plot was selected for this study.

No grafting between trees in the vertical system was noted. However, it did happen within trees, sometimes frequently (Fig. 11), and was likely facilitated by the compactness of the soil and the tendency of roots to penetrate the same cleavage planes. All measured trees, except two, had grafts amongst their verticals.

## Foliage Weights and Foliage Weight:Root Length Ratios

Foliage weights ranged across treatments from 1.4 to 5.0 kg for three intermediate and suppressed trees and 8.4 to 41.8 kg for 13 codominants and dominants. They averaged nearly 12.5 kg per tree less in the permanent A treatment than in the control (Table 6), a significant difference at 0.05 when only these two treatments alone were tested in an analysis of variance. Inclusion of the other two treatments in the analysis introduced considerable variation and resulted in significance at the 20% level. Distribution of foliage by years within dominant trees did not differ significantly among treatments, although the percentages shifted to higher levels of older (1962-64) foliage in the seasonal and permanent B treatments.

Significant differences among treatments were not found when ratios of foliage weight to lengths of any portion of the root system were used as the response variable. The ranges among treatments considerably overlapped, attributable in part to the extreme ranges in root lengths.

## Soil Moisture Status

Precipitation during the growing season in northern Idaho is limited; for example, annual precipitation near the study site averaged 83.1 cm from 1956 through 1967 and 8.1% of it fell in May, 6.8 in June, 2.4 in July, 3.9 in August, and 4.3 in September. From mid-June to mid-September, much of the rain falls as showers and rarely gets to the mineral soil.

As measured between the spring and fall samples for the upper 183 cm of soil profiles in all plots, loss of soil moisture did not differ significantly between the control and seasonal treatments, despite an average of 9 cm of rain potentially available to the control but not the seasonal plot between samplings. However, both treatments used significantly greater amounts of water between sample dates than either of the other two. Also, the permanent A plot lost significantly less water than the permanent B one. These differences for the entire profile of all treatments (Table 7) are best illustrated by Fig. 12 which shows the amount of water in only the upper 61 cm. This horizon accounted for much of the variation encountered for the entire profile. Differences among years were not significant. The effect of a leaking shelter for the permanent B plot during the winter of 1959-60 is evidenced by a much higher spring sample for 1960 than for all years except 1956, the year of installation.

## DISCUSSION

Water deficits reduce the rates of many physiological processes influencing growth of stems, foliage, and roots of trees; but it is equally axiomatic that quantitative expression of this reduction has been subject to much controversy (14). Variation in the parameters of studies of moisture-stress effects on tree growth unquestionably explain such controversy; for example, how often does one encounter study of trees of the size and species growing in environments equivalent to this experiment? It is small wonder that one might speculate on certain conclusions drawn for his observations in reference to studies of others. That speculation in science and its use here are valid is left for others to debate.

The single consistent effect of sustained moisture stress on the young mature white pine trees of this study was a reduction in height and radial increment. Finding that these classical stress-growth correlations were consistent with other observations, we were surprised that so few other features of the stressed trees consistently and significantly differed from the unstressed ones. Presumably, the manufacturing and transpiration component (foliage) or the absorbing component (roots) or some combination thereof might mirror their product (wood production). Foliage weights were significantly smaller on the permanent A trees than the control ones, but the treatment response may have been an artifact. The small number of trees and their smaller average size probably masked any real differences in amount of foliage between stress and non-stress trees. As with foliage, comparisons of all or portions of the root system in pre-stress vs. stress conditions were impossible because no measure of pre-stress condition was collected. Also, measurements of the root systems did not include the principal absorbing portion, i.e., less than 2 mm in diameter, because the combination of compact soil and the washing process stripped most roots of this size from their parent root. Whether a higher proportion of these roots were living and functional in the non-stress than stress environments is unknown although previous studies (4) suggest that might be the case.

The very dry environment of the lateral absorbing systems in the continuously covered plots (permanent A and B) versus the periodically replenished moisture environment of the control and seasonal plots obviously reflect distinguishable differences among plot environments. The effective absorbing portion of the verticals was in a moist regime throughout the year (Table 7 and Fig. 8) regardless of treatment. A reduced food supply on the permanent plots could have contributed to differences in height and radial increments and foliage weight. If variable food supply contributed to the radial growth differences, then it could also be expected to affect root mass. Whether the absence of demonstrable treatment effects on roots was due to there being no reduction in root growth or to differences in the relative reaction of stems and roots to reduced moisture and carbohydrates cannot be explained by available data. On the contrary, our data strongly suggest, but do not prove, that reduced terminal and radial growth of stressed trees was the direct result of reduced moisture supply to the lateral roots.

A second outstanding feature of the study trees, consistent with our general observations elsewhere, was the extreme dependency of treated trees on their vertical roots for survival. The upper soil horizon of 30.5 cm contained nearly all of the lateral roots regardless of treatment. Because this horizon could not be recharged except by capillary action in the permanent A and B plots, the small amounts of water loss between sampling periods (Table 7) means that (1) little, if any, water was supplied the trees by lateral roots in this particular horizon, and (2) the moisture present in it was mostly unavailable for tree use. The latter is further supported by the small differences between moisture at fall sampling and wilting coefficient in the three stress treatments (Table 7). Conversely, there were substantially larger differences at the two deepest 30.5-cm horizons. Though these two horizons lost more moisture than the uppermost one, they were frequently still moist in the fall. The spring samples were very moist, sometimes difficult to remove from these depths by the king tube because of that. Undoubtedly, moisture was moving through the sand lenses from upslope sources and recharging the lower horizons throughout much of the year. The water loss in these horizons between spring and fall is, therefore, not indicative of total water loss, in contrast to the situation in the uppermost horizons.

Grafting between trees was not frequent. When it occurred, the trees appeared to have benefited merely because their moisture supply surface had been expanded. On the other hand, such grafting could have been detrimental to one or the other tree had virulent root pathogens, like Verticicladiella spp., occupied portions of the grafted system. In the case of the white pine on the seasonal plot to have lost nine of its 23 verticals, grafting amongst the verticals, as in Fig. 11, could have led to their demise earlier than normal once one root became infected by A. mellea since all were grouped centrally off the root collar. However, when we excavated this tree's roots, they had been decayed to the point that no evidence of grafting could have been detected. This study and others (9) indicate no relationship of grafting between trees to the onset or intensification of pole blight.

Our data should caution those prone to such a statement as "stress trees are more susceptible to bark beetle attack than are nonstress ones." Whatever is implied by stress, one frequently infers that it is induced by drought or by a root system impaired, for example, by root disease. We know that stress was sufficient to reduce growth of the stem. Apparently insufficient stress was induced to bring about mountain pine beetle (Dendroctonus ponderosae Hopk.) attacks even though other attacks on the Experimental Forest showed beetle populations were present during this period. Therefore, we merely conclude that the stress was insufficient, if in fact stress alone is enough cause, for beetle attack.

When the experiment was started in 1955, we did not recognize that pole blight had run its course in this particular stand. Although that fact subsequently became apparent, the reason(s) for it are not clear. Other studies suggest that greater than usual drought during the period 1916 to 1940 may have been instrumental in the cause of pole blight (7,12). Perhaps in the absence of such drought conditions, even the level of soil moisture stress induced experimentally was insufficient to cause all the symptoms of pole blight. Furthermore, reduced amounts of moisture supplied by deep roots may be prerequisite to development of sufficient stress to induce all symptoms of the disease. It is noteworthy that excavation of trees with lesions, considered to be the most definitive of the symptoms (1,11), showed that a large proportion of the vertical roots were dead (9).[1/] In the case of our study trees, a supply of moisture to the vertical roots appeared to have been sufficient to sustain life and health adequately so that no bark beetle attacks occurred and only some pole blight symptoms (increment and foliage reduction) developed. Whether other factors are requisite for either is conjectural. At the start, we believed that the effect of drought on pole size trees should be tested; that we might even induce the disease. Had we known that subsurface moisture recharge on this site would become a significant factor, we would have chosen a different site. As it was, we achieved partial symptom expression from partly stressed trees.

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[1/] Also McMinn, R. G. 1956. Unpublished data.

Special thanks are due Mr. M. A. Grismer, Pacific Forest Research Centre, Canadian Forestry Service, Victoria, B.C., for his able supervision of the hydraulic excavation of root systems and collection of root data.

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## FIGURE CAPTIONS

Figure 1. Permanent A plot showing distribution of trees 1 through 10, trunk collars, and square access holes in the wooden shelter. A 1-m deep trench occurs just under the shelter eaves and discharges to the lower right.

Figure 2. Control plot showing lower stems of trees 1 through 11 just before tree felling. The extent of thinning at the beginning of the experiment can be judged by comparison of the stand behind the plot.

Figure 3. Permanent A plot prepared for root washing with support logs attached to stumps.

Figure 4. Upper crown of a tree from the permanent A plot. The 1955 stem growth segment is the one above the man's right hand. Note reduced growth from 1956 through 1967 compared to preceding several years on both stem and branches.

Figure 5. Deviations in the mean annual radial growth at 3.5 m by treatment, for the period from 1944 through 1967.

Figure 6. Vertical roots of a dominant tree from the permanent B plot. Root diameters reduce sharply from the 25-cm to the 100-cm depth, thus, producing a club-shaped root. Markers on the tape are at 25-cm intervals, the first is at 25 cm.

Figure 7. Excavated permanent B plot showing vertical roots of a dominant tree (left) and a suppressed one (right) and the narrow sandy lenses (arrow) in an otherwise dense silty clay horizon several meters deep.

Figure 8. Vertical roots of a dominant tree in the permanent B plot developing horizontally in sandy lenses between silty clay soil layers. Markers on the tape are at 25-cm intervals.

Figure 9. Two trees of the seasonal plot. The contrasting lateral systems are supported by wires stretched between support poles.

Figure 10. Grafts (arrow) in the permanent A plot between lateral roots within a tree (1) (right side of support pole), between trees (2) (left side of support pole), and between a live tree and a tree (3) (lower right corner) which died prior to shelter construction. Root system of the dead tree was still living when excavated.

Figure 11. Grafts between vertical roots of a dominant tree in the seasonal plot. These roots were quite flattened and within the same vertical plane when excavated.

Figure 12. Centimeters of water in the 0-30.5-cm and 30.6-61.0-cm soil horizons by treatment, year, and season of sampling.

TABLE 1. Average annual radial growth of white pine at 5 positions on the stem and average annual terminal growth by treatment for 1944-1955 (prestress) and 1956-1967 (stress).

| | | | Position on Tree Bole | | | | | |
|---|---|---|---|---|---|---|---|---|
| Treatment | No. of Trees[1/] | Growth Period | 0.5 Meters | 3.5 Meters | Bottom Crown | Mid Crown | Top Crown | Terminal Growth |
| | | Years | - - - - - - | - - - - - - | mm | - - - - - - | - - - - - - | Cm |
| | | 1944-55 | 1.42 | 1.19 | 1.15 | 1.65 | 2.17 | 28.9 |
| Control | 5 | 1956-67 | 1.52 | 1.14 | 1.02 | 1.28 | 1.74 | 26.3 |
| | Difference (%) | | +7 | -4 | -11 | -22 | -17 | -9 |
| | | 1944-55 | 1.29 | 1.03 | 1.04 | 1.44 | 2.07 | 27.5 |
| Permanent A | 5 | 1956-67 | 0.87 | 0.57 | 0.50 | 0.64 | 0.87 | 11.4 |
| | Difference (%) | | -33 | -45 | -52 | -56 | -58 | -59 |
| | | 1944-55 | 2.95 | 1.71 | 1.39 | 2.39 | 2.89 | 31.9 |
| Permanent B | 2 | 1957-67 | 1.24 | 1.09 | 0.74 | 1.08 | 1.33 | 15.9 |
| | Difference (%) | | -58 | -36 | -47 | -55 | -54 | -50 |
| | | 1944-55 | 1.10 | 0.99 | 1.06 | 1.38 | 1.92 | 23.7 |
| Seasonal | 2 | 1957-67 | 0.81 | 0.88 | 0.87 | 1.22 | 1.33 | 18.5 |
| | Difference (%) | | -26 | -11 | -18 | -12 | -31 | -22 |

[1/] Dominant and codominant trees only

TABLE 2. Treatment mean values of annual basal area increment (ABAI) of the stress period (1956-67) ÷ ABAI of prestress period (1944-55).

| Treatment | No. of trees | Means |
|---|---|---|
| Permanent B | 3 | .557[a] |
| Permanent A | 10 | .673[a] |
| Control | 10 | .856[b] |
| Seasonal | 3 | .923[b] |

[a,b]Means not followed by the same letter differ significantly at 0.01 (the error mean square is .017).

TABLE 3. Average annual radial increment at 3.5 m for western redcedar, western larch, and Douglas-fir in different treatments in prestress (1944-55) and stress (1956-67) periods.

| | | Radial Increment (mm) | | | | | |
|---|---|---|---|---|---|---|---|
| | | Western Redcedar | | Western Larch | | Douglas-fir | |
| Treatment | Period | No. of Trees | Increment | No. of Trees | Increment | No. of trees | Increment |
| Control | Prestress | 4 | 1.27 | 1 | 0.90 | 1 | 1.18 |
| | Stress | | 1.19 | | 0.72 | | 0.92 |
| | Difference | | -6% | | -20% | | -22% |
| Permanent B | Prestress | 8 | 1.16 | 3 | 0.93 | 3 | 0.78 |
| | Stress | | 0.36 | | 0.28 | | 0.28 |
| | Difference | | -69% | | -70% | | -64% |
| Seasonal | Prestress | 4 | 1.35 | 2 | 0.83 | 1 | 0.79 |
| | Stress | | 1.00 | | 0.42 | | 0.55 |
| | Difference | | -26% | | -49% | | -30% |

TABLE 4. Mean tree root length (cm) and mortality of lateral and vertical roots by treatment and root diameter classes

| Treatment | Number of Trees[1/] | Root Type and Diameter Class (cm) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Lateral | | | | | | Vertical | | |
| | | 0.2-<0.5 | 0.5-<1.0 | 1.0-<2.0 | 2.0-<5.0 | 5.0-<10.0 | >10 | 0.2-<0.5 | 0.5-<1.0 | >1.0 |
| Control | 3 | | | | | | | | | |
| 39.0 & 41.6* | | | | | | | | | | |
| Length (cm) | | 48,984 | 32,581(a)[2/] | 15,878 | 4,064 | 520 | 497 | 20,005 | 8,418 | 11,694 |
| Mortality (%) | | 18.9(a,b)[2/] | 8.0 | 5.1 | 1.2 | 0.0 | 0.0 | 8.3 | 7.3 | 0.2 |
| Permanent A | 5 | | | | | | | | | |
| 31.8 & 30.0* | | | | | | | | | | |
| Length (cm) | | 29,980 | 11,053(c) | 9,282 | 2,469 | 425 | 258 | 15,071 | 6,152 | 8,755 |
| Mortality (%) | | 25.0(a,b) | 18.8 | 9.4 | 2.9 | 5.6 | 0.0 | 6.4 | 6.8 | 0.2 |
| Permanent B | 2 | | | | | | | | | |
| 33.6 & 40.0* | | | | | | | | | | |
| Length (cm) | | 51,454 | 23,017(a,b) | 10,337 | 3,561 | 871 | 343 | 29,477 | 9,999 | 17,998 |
| Mortality (%) | | 46.6(a) | 18.9 | 5.0 | 1.1 | 0.0 | 7.1 | 7.1 | 2.9 | 0.3 |
| Seasonal | | | | | | | | | | |
| Seasonal | 2 | | | | | | | | | |
| 34.7 & 36.8* | | | | | | | | | | |
| Length (cm) | | 34,704 | 15,091(b,c) | 11,611 | 3,309 | 610 | 144 | 25,818 | 11,922 | 13,514 |
| Mortality (%) | | 5.7(b) | 8.2 | 4.4 | 0.0 | 14.3 | 0.0 | 1.7 | 0.5 | 0.2 |

[1/]Dominant and codominant classes only.

[2/]Means not followed by the same letter differ significantly at 0.01; all other values were not significantly different.

*Average height (m) and diameter (cm), respectively.

TABLE 5. Percentages of vertical roots penetrating successive 50-cm soil depths by treatments and 0.5 and 1.0 cm diameters

| Soil | Control (48)[1/] | | Permanent A (57) | | Permanent B (106) | | Seasonal (43) | |
|---|---|---|---|---|---|---|---|---|
| Depth | 0.5 | 1.0 | 0.5 | 1.0 | 0.5 | 1.0 | 0.5 | 1.0 |
| Cm | Percent | | | | | | | |
| 50 | 100.0 | 100.0 | 100.0 | 99.6 | 100.0 | 100.0 | 100.0 | 100.0 |
| 100 | 90.2 | 84.6 | 59.4 | 51.9 | 70.3 | 60.4 | 90.8 | 90.8 |
| 150 | 40.6 | 31.5 | 18.4 | 13.4 | 24.1 | 22.2 | 56.3 | 48.4 |
| 200 | 9.8 | 6.3 | 6.7 | 4.6 | 4.2 | 2.8 | 34.5 | 28.7 |
| 250 | -- | -- | 3.2 | 0.7 | 2.4 | 0.5 | 25.3 | 16.1 |

[1/] Average number of roots per tree in each treatment on which percentages are based.

TABLE 6. Average foliage weights and percentages of the average by year of foliage origin, by treatment and tree dominancy class

| Treatment | Dominance Class[1/] | No. Trees | Foliage Weight | Percentage of Weight by Year 1967 | 1966 | 1965 | 1962-64 |
|---|---|---|---|---|---|---|---|
| | | | Kg | - - - - - - Percent | | | - - - - - |
| Control | 1&2 | 3 | 27.6 | 33.9 | 33.8 | 24.8 | 7.5 |
| | 3&4 | 1 | 1.4 | 43.3 | 38.1 | 16.0 | 2.6 |
| Permanent A | 1&2 | [2/]6 | 15.1 | 36.1 | 32.3 | 23.6 | 8.0 |
| | 3&4 | 1 | 5.0 | 30.6 | 24.1 | 22.9 | 22.4 |
| Permanent B | 1&2 | 2 | 29.1 | 31.9 | 24.1 | 26.6 | 17.4 |
| | 3&4 | 0 | -- | -- | -- | -- | -- |
| Seasonal | 1&2 | 2 | 25.1 | 28.7 | 27.1 | 26.1 | 18.1 |
| | 3&4 | 1 | 3.5 | 37.2 | 31.2 | 21.2 | 10.4 |

[1/] 1 = dominant, 2 = codominant, 3 = intermediate, and 4 = suppressed.

[2/] Two of these trees are represented as one tree in Table 4 because their root systems were integrally grafted.

TABLE 7. Nine-year means of available soil water at various depths at beginning and end of growing season in different treatments.

| Treatment | Depth of Available Water (cm)* | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Soil Depths (cm) | | | | | | | | | | | |
| | 0 - 30.5 | | 30.6 - 61.0 | | 61.1 - 91.5 | | 91.6 - 122.0 | | 122.1 - 152.5 | | 152.6 - 183 | |
| | Spring | Fall | Spring | Fall | Spring | Fall | Spring | Fall | Spring | Fall | Spring | Fall |
| Control | 9.4 | 2.6 | 4.5 | 2.1 | 5.5 | 3.7 | 5.2 | 3.9 | 6.9 | 4.9 | 8.3 | 5.7 |
| Permanent A | 2.3 | 1.4 | 2.6 | 2.0 | 3.4 | 3.1 | 5.2 | 4.7 | 5.1 | 3.7 | 6.7 | 3.7 |
| Permanent B | 2.8 | 1.5 | 3.8 | 1.2 | 3.9 | 1.8 | 4.7 | 2.4 | 7.2 | 5.6 | 6.7 | 5.3 |
| Seasonal | 5.4 | 1.4 | 5.9 | 2.8 | 5.1 | 2.5 | 4.5 | 1.3 | 7.0 | 4.9 | 7.9 | 6.5 |

*Depth of available water equals field moisture values less 15 bar percentage.